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Amidohydrolase activity, soil N status, and the invasive crucifer *Lepidium latifolium*

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Abstract

Wetlands and riparian habitats in the western United States are being invaded by the exotic crucifer *Lepidium latifolium* (perennial pepperweed, tall whitetop). It was hypothesized that *L. latifolium* was an effective competitor due to its ability to make available and take up more nitrogen than vegetation it is replacing. The hypothesis was tested by comparing amidohydrolase activities, available soil N, 30 day aerobic N-mineralization rates, and plant uptake of N in paired *L. latifolium* invaded and non-invaded plots occupied by *Elytrigia elongata* (tall wheatgrass). Attributes were measured by date (June 1998, September 1998, April 1999, and May 2000) and by soil depth (0–15, 15–30, 30–50, and 50–86 cm). *Lepidium latifolium* invaded sites had significantly ($p \leq 0.05$) greater urease, amidase, glutaminase, and asparaginase activities than sites occupied by *E. elongata* for most dates and soil depths. In addition, despite far greater uptake of N per unit area, *L. latifolium* sites still had significantly greater available N and N-mineralization potentials than *E. elongata* for most dates and depths. In general, enzyme activities significantly correlated with available soil N, with a stronger relationship for sites invaded by *L. latifolium*. There were few significant linear correlations of enzyme activities with net N mineralization potentials for *L. latifolium* sites, but many for sites occupied by *E. elongata*. These data support the working hypothesis.

Introduction

The exotic crucifer *Lepidium latifolium* L. (perennial pepperweed), a native of southeastern Europe and Asia, has become widely distributed in wetland and riparian habitats throughout the western United States (Young et al., 1995). Plants vary from 0.4 to 1.0 m tall, with a multitude of stems forming dense thickets. The plants are clonal and have extensive underground, budding rootstocks that radiate in all directions from newly established plants. In 2 seasons, a single established plant becomes a small population that can be several meters in diameter. In as few as 5 years, infestations can be near monospecific with stem densities approaching 150 m^{-2}. Roots of *L. latifolium* are coarse, widely-spaced, and extend vertically more than 3 m into the soil. *L. latifolium* has successfully invaded a multitude of soil types from coarse-textured, neutral pH, riverain deposits, to finer textured saline/alkaline sediments. A variety of plant communities have been invaded; from naturally flooded and irrigated native pastures and haylands, managed pastures planted to grasses, and native undisturbed *Sarcobatus vermiculatis/Distichlis spicata*, and *Carex/Juncus* communities.

Do these diverse ecosystems have some common characteristic which explains invasion by *L. latifolium*? Alternatively, does *L. latifolium* have a unique strategy which enhances its competitive stature in a multitude of habitats? Disturbance and increased availability of soil resources are two factors used to explain community invasibility (Burke and Grime, 1996). In particular, available soil N is a major factor controlling competitive interactions among plants and is a critical determinant in ecosystem invasibility (McLendon and Redente, 1992; Vitousek et al., 1987).

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Moreover, specific plant species can differentially affect the availability and the timing of availability of soil N (Burke, 1989; Bolton et al., 1990; Wedin and Tilman, 1990). Based on this literature and field observations of *L. latifolium*, a working hypothesis was formulated: *L. latifolium* may increase soil nitrogen availability, relative to plants it is replacing. This paper reports on results of field studies to test this hypothesis.

Materials and methods

The study area

Research was conducted at the Honey Lake Wildlife Refuge in northeastern California approximately 74 km north-northwest of Reno, Nevada, USA. Honey Lake, at an elevation of 1234 m, is a remnant of the immense Pleistocene Lake Lahontan which covered much of northwestern Nevada and adjacent California (Morrison, 1991). Parent materials of the dry lake bottoms are largely fine-textured, saline, lacustrine sediments with local influence by eolian deposits and reworked, coarse-textured, beach and offshore deposits. The topography is nearly level to very gently undulating and is interrupted by low swales associated with the distributary system of the Susan River. Honey Lake is arid, averaging 23–30 cm of precipitation per year. The area is frequently flooded by spring snowmelt from the Sierra-Cascade mountains to the west via the Susan River. Native vegetation includes black greasewood (*Sarcobatus vermiculatus* [Hook.] Torrey), inland saltgrass (*Distichlis spicata* [L.] E. Greene), basin wildrye (*Leymus cinereus* Schribner & Merr.), and sedges (*Carex* spp.) and rushes (*Juncus* spp.). Land use includes pasture, hayland, and cropland.

Invasion by *L. latifolium* began in the mid 1980s and by the early 1990s most stream channels of the Susan River, along with the sides of irrigation control ditches, were completely occupied by *L. latifolium*. This weed has since expanded to agronomic fields and native plant communities causing concern over loss of nesting habitat for migratory waterfowl (Personal communication, Chuck Holms unit manager). In 1993, studies were initiated at the Fleming Unit (N 40° 21′ 188″; W 120° 18′ 148″) in a 32 ha field that had been planted with the grass *Elytrigia elongata* Host (Nevski) in 1987 for nesting habitat. At this time, the stand of *E. elongata* was healthy and robust and *L. latifolium* plants were limited to an irrigation ditch that marked the western edge of the field. In 1994, we marked out a 40 m^2 plot in the field to inventory the spread of *L. latifolium*, at which time, there were two < 1 m^2 colonies with stem densities of <10 m^{-2}. In our year 2000 inventory, most of the 40 m^2 plot had become invaded with stem densities >100 m^{-2} (summarization of these data can be seen at wric.ucdavis.edu/exotic/techtran/rate_of_spread.htm). The entire agronomic field is mapped as the Humboldt series, a fine, smectitic, calcareous, mesic, Fluvaquentic Endoaquolls (Table 1).

Table 1. Pedon description of site occupied by *L. latifolium*

Horizon	Depth (cm)	Texture	Munsell color	
			Dry	Moist
Oi	0-+5			
A1	0–8	silty clay loam	10YR 4/1	10YR 2/1
A2	8–20	silty clay loam	10YR 4/1	10YR 2.5/1
Bw	20–46	silty clay	10YR 4/1	10YR 3/1
Bgy	46–81	silty clay	5Y 4/1	5Y 2.5/1
C1g	81–127	silty clay	5Y 5/1	5Y 3/1
C2g	127–178	silty clay	5Y 5/1	5Y 3/1

All horizons slightly effervesce upon addition of 1N HCl. Abbreviations: i = undecomposed plant litter; w = cambic or slightly altered; g = gleyed; y = visible crystals of gypsum. At this location, roots of *L. latifolium* exceeded 3 m in depth.

Data collection

A paired plot design was used. Plots (4 replicates) were sampled in June 1998, September 1998, April 1999, and May 2000. For growth of *L. latifolium*, these dates correspond to: maximum growth phase, past flowering, initiation of growth, and maximum growth phase, respectively. Sites were on both sides of an invasion front leaving a >2 m buffer between the paired sites. Paired plots were moved to different places for each time of sampling. Rapid advancement of the invasion front occurred during years of surface flooding. Spring surface flooding during the period of data collection was minimal, thus our time series of data collection also represents greater time of occupation by *L. latifolium*. Soil samples from four depth increments were collected and homogenized: 0–15, 15–30, 30–50, and 50–86 cm. Samples were kept moist, returned to the laboratory and refrigerated at 2 °C until all attributes were measured. Attributes were measured on the <2-mm size fraction and included organic carbon (dichromate digestion – Nelson and Sommers,

Table 2. Soil KCl-extractable N and net 30 day aerobic N-mineralization potential by microsite, soil depth, and date of sampling

Depth	June 1998		Sept 1998		April 1999		May 2000	
(cm)	LELA	ELEL	LELA	ELEL	LELA	ELEL	LELA	ELEL
	KCl-extractable N (mmol/kg)							
0–15	0.112	0.072	0.192	0.094	0.216	0.156	0.156	0.094
15–30	0.118	0.039	0.116	0.043	0.174	0.106	0.161	0.054
30–50	0.078	0.012	0.060	0.022	0.175	0.041	0.091	0.027
50–86	0.045	0.018	0.061	0.006	0.058	0.016	0.040	0.008
	ANOVA: microsite × depth $p < 0.0001$							
	0–15 cm		15–30 cm		30–50 cm		50–86 cm	
LELA	0.154 (0.128–0.186)		0.133 (0.111–0.159)		0.089 (0.074–0.107)		0.047 (0.035–0.064)	
ELEL	0.096 (0.080–0.115)		0.053 (0.044–0.063)		0.018 (0.011–0.028)		0.009 (0.006–0.013)	
	net 30 day aerobic N mineralization potential (mmol/kg)							
0–15	1.492	0.529	0.168	−0.006	0.595	1.204	0.242	0.178
15–30	0.740	0.305	0.202	0.004	0.836	0.684	0.313	0.054
30–50	0.455	0.181	0.038	−0.017	0.247	0.179	0.327	0.058
50–86	0.235	0.019	0.074	−0.003	0.235	0.106	0.225	0.060
	ANOVA: microsite × depth $p = 0.0404$							
	0–15 cm		15–30 cm		30–50 cm		50–86 cm	
LELA	0.465 (0.278–0.778)		0.436 (0.225–0.843)		0.241 (0.144–0.402)		0.105 (0.043–0.256)	
ELEL	0.320 (0.191–0.535)		0.103 (0.047–0.225)		0.036 (0.019–0.070)		0.023 (0.013–0.039)	
	ANOVA: microsite × date $p = 0.0152$							
	June 1998		September 1998		April 1999		May 2000	
LELA	0.466 (0.205–1.058)		0.119 (0.053–0.267)		0.276 (0.138–0.553)		0.333 (0.220–0.505)	
ELEL	0.175 (0.112–0.273)		0.011 (0.006–0.022)		0.257 (0.115–0.576)		0.055 (0.028–0.110)	

Abbreviations: LELA – *L. Latifolium*; ELEL – *E. elongata*. Primary data are means of replications by date, depth and microsite. Only statistically significant interactions including microsite are presented for which confidence intervals (95%) are displayed in parentheses.

1982), Kjeldahl N (Bremner and Mulvaney, 1982). Potassium chloride was used to extract available NO_3^- and NH_4^+ (Bundy and Meisinger, 1994). Nitrogen mineralization potential was gaged via a 30 day aerobic incubation in the dark (Hart et al., 1994). Four amidohydrolases were assayed using standard procedures: L-asparaginase, L-glutaminase, amidase, and urease (Tabatabai, 1994). Available N and enzyme assays were conducted within one week. All values were corrected to oven dry weight (105 °C). A pressure plate apparatus was used to determine available moisture content (0.033–1.5 MPa). In September 1998, vegetation samples were collected by randomly locating 4 paired invaded/non-invaded plots (*L. latifolium* and *E. elongata*). We did not sample in the >5 m buffer zone at the invasion front. At this time, *L. latifolium* had completed flowering and the grasses were beginning to senesce. Using a one-half meter tape, we inscribed a circle, and harvested all live vegetation inside the circle to ground level. Plant tissue was dried at 60 °C and ground in a Udy mill prior to elemental analyses. A Leco analyser was used to quantify tissue N.

Statistics

Soil data were analyzed using split-split plot analysis of variance model with categorical variables date (June 1998, September 1998, April 1999, and May 2000), and microsite (*L. latifolium* invaded, non-invaded occupied by *E. elongata*) with repeated measures on soil depth (0–15, 15–30, 30–50, and 50–86 cm). Variance stabilizing transformations were used for all response variables. Urease, glutaminase and amidase were transformed by square roots; asparaginase, KCl-extractable N and net 30 day mineralization potentials were transformed by natural logs. Only main effects or interactions including microsite are presented for which confidence intervals (95%) are shown to discern differences among means. Correlation matrixes were

Table 3. Biomass, live tissue N content, and N uptake for *L. latifolium* and *E. elongata*. Plants harvested in September 1998

Plant	Dry biomass ($g\ m^{-2}$)	N content (%)	N uptake ($g\ m^{-2}$)
L. latifolium	400	0.612	3.09
E. elongata	123 *	0.647	0.95 *

An asterisk denotes significant difference between plants at the $p \leq 0.05$ level (Fisher's Protected LSD). Biomass, N content, and N uptake based on live biomass.

used to evaluate relationships among % organic C, % N, and enzyme activities with Fisher's r to z transformation used to judge significance. Graphs were constructed to display least squares linear regression lines, by plant species and soil depth, between available N and enzyme activities and between net N mineralization potentials and enzyme activities. Plant data were analyzed with a one way analysis of variance with categorical variable microsite. Mean separation used Fisher's protected least significant difference.

Results

Available soil N, N mineralization potentials, and plant N

Microsite significantly interacted with soil depth for available N and net 30 day N mineralization potentials (Table 2). Sites invaded by *L. latifolium* had significantly ($p \leq 0.05$) greater available N for all soil depths and greater net N mineralization potentials, for all soil depths except 0–15 cm, than corresponding values for *E. elongata* occupied sites. Especially noteworthy are the magnitude of differences in available N and net N mineralization potentials between *L. latifolium* and *E. elongata* at depths between 30 and 86 cm. Net 30 day N mineralization potentials were also influenced by a significant microsite by depth interaction in which *L. latifolium* invaded sites had greater N mineralization potentials for the September 98 and May 00 dates than did *E. elongata* occupied sites. After the growing season in 1998, available N and net N mineralization potentials remained very high below *L. latifolium* occupied sites and *E. elongata* occupied sites had net negative N mineralization potentials for three depths. At plant maturity in 1998, tissue N content was statistically similar between *L. latifolium* and *E. elongata*, but on a per area basis, *L. latifolium* produced nearly 3.5 times greater biomass and accumulated over 3 times more N than did *E. elongata* (Table 3). Information from other sites and other years indicates that *L. latifolium* consistently produces far more biomass per unit area than vegetation it is replacing (unpublished data, USDA-ARS Reno, NV research group).

Enzyme activities

Activities of the amidohydrolase enzymes urease, glutaminase and asparaginase were influenced by a significant microsite by soil depth by date interaction (Table 4). Soil urease activity was least influenced by microsite, but sites invaded by *L. latifolium* had statistically greater activity for several dates and soil depths. Invasion by *L. latifolium* resulted in statistically greater soil enzyme activities of glutaminase, and asparaginase for most dates and soil depths than corresponding values for *E. elongata* occupied sites. In general, the least difference in enzyme activities between vegetation types occurred in the April 1999 set with the greatest difference occurring in the September 1998 set. Soil amidase activities were influenced by significant microsite by soil depth and microsite by date interactions (Table 4). For most soil depths and dates, amidase activity was significantly greater on *L. latifolium* invaded sites.

Enzyme activity relationships

For both *L. latifolium* invaded and non-invaded sites, there were highly significant positive linear correlations between enzyme activities and total soil N and organic C (Table 5). Correlation coefficients were generally higher for *L. latifolium* invaded sites. Enzyme activities significantly correlated with each other (Table 5). Paired enzyme relationships for *L. latifolium* generally had higher correlation coefficients than for *E. elongata*. Carbon: N ratios of the soil were not significantly different between plant microsites and soil depth (Table 6) and in general, C:N ratios did not correlate significantly with enzyme activities (Table 5).

Overall, enzyme activities of urease, glutaminase, and asparaginase significantly and positively correlated with available soil N for both *L. latifolium* and *E. elongata*; R^2 values were, overall, much lower for amidase and for soil depth 50–86 cm (Figure 1). The relationship of available-N to enzyme activities was much stronger for *L. latifolium* sites and strongest in the 30–50 cm depth increment. Surprisingly, the strong positive correlation between enzyme activity

Table 4. Soil amidohydrolase activities by microsite, soil depth and date of sampling

Depth (cm)	June 1998		Sept 1998		April 1999		May 2000	
	LELA	ELEL	LELA	ELEL	LELA	ELEL	LELA	ELEL
	Urease actiivty (μmoles/g/hr, ANOVA: microsite × depth × date, $p = 0.0404$							
0–15	7.4 (6.0–9.0)	6.4 (5.1–7.9)	11.3 (9.5–13.2)	8.4 (6.8–10.0)	10.6 (8.8–12.4)	13.7 (11.7–15.7)	9.3 (7.7–11.1)	5.2 (4.0–6.5)
15–30	11.4 (9.6–13.3)	10.0 (8.3–11.8)	10.8 (9.1–12.7)	6.3 (5.0–7.7)	14.5 (12.5–16.7)	14.3 (12.3–16.5)	10.5 (8.8–12.3)	7.6 (6.1–9.1)
30–50	5.3 (3.6–7.5)	3.3 (1.9–5.0)	4.3 (2.7–6.2)	3.2 (1.8–4.9)	11.7 (8.9–14.8)	6.5 (4.5–8.8)	7.5 (5.2–9.8)	2.3 (1.2–3.8)
50–86	1.4 (0.8–2.3)	1.3 (0.7–2.0)	1.7 (1.1–2.5)	1.0 (0.5–1.6)	4.0 (3.0–5.2)	3.1 (2.2–4.1)	1.4 (0.9–2.2)	0.7 (0.3–1.2)
	Glutaminase activity (μmoles/g/hr), ANOVA: microsite × depth × date, $p < 0.0001$							
0–15	13.1 (10.7–15.7)	9.3 (7.3–11.5)	22.6 (19.4–26.0)	1.1 (0.5–1.9)	19.1 (16.2–22.2)	19.3 (16.3–22.3)	16.4 (13.7–19.2)	3.8 (1.1–8.2)
15–30	12.3 (10.0–14.8)	4.7 (3.1–6.5)	15.5 (9.2–23.5)	0.6 (0.2–1.4)	19.4 (16.5–22.5)	12.7 (10.4–15.3)	15.7 (13.1–18.6)	0.2 (0.0–0.6)
30–50	5.7 (2.2–10.9)	1.4 (0.1–4.3)	5.0 (1.8–9.9)	0.3 (0.1–0.8)	17.2 (10.5–25.5)	2.6 (0.5–6.3)	5.6 (2.2–10.7)	0.2 (0.0–0.6)
50–86	0.6 (0.1–1.4)	0.3 (0.1–0.8)	1.7 (0.1–4.9)	0.6 (0.2–1.3)	4.1 (1.2–8.5)	0.5 (0.5–1.1)	0.3 (0.1–0.8)	0.1 (0.0–0.4)
	Asparaginase activity (μmoles/g/hr), ANOVA: microsite × depth × date, $p = 0.0352$							
0–15	1.35 (0.87–2.08)	0.47 (0.31–0.73)	2.12 (1.37–3.29)	0.45 (0.29–0.69)	2.35 (1.52–3.65)	1.51 (0.97–2.34)	2.20 (1.42–3.41)	0.85 (0.55-1.31)
15–30	0.78 (0.51–1.21)	0.37 (0.24–0.57)	1.00 (0.63–1.50)	0.18 (0.12–0.28)	1.62 (1.05–2.51)	0.67 (0.43–1.04)	1.84 (1.19–2.86)	0.31 (0.20–0.48)
30–50	0.17 (0.11–0.26)	0.09 (0.06–0.13)	0.24 (0.15–0.36)	0.08 (0.05–0.14)	1.07 (0.69–1.66)	0.19 (0.12–0.29)	0.56 (0.36–0.87)	0.08 (0.05–0.13)
50–86	0.07 (0.04–0.11)	0.03 (0.02–0.05)	0.12 (0.08–0.19)	0.06 (0.04–0.09)	0.21 (0.14–0.33)	0.09 (0.06–0.14)	0.13 (0.08–0.20)	0.04 (0.03–0.07)
	Amidase activity (μmoles/g/hr)							
0–15	15.7	15.4	24.6	16.4	14.3	11.1	19.7	15.5
15–30	14.6	13.9	16.2	10.9	13.6	8.1	19.4	11.3
30–50	1.8	1.4	4.2	1.8	6.3	0.7	8.5	0.3
50–85	0.1	0.1	1.6	0.1	0.5	0.2	0.2	0.1
	ANOVA: microsite × depth, $p = 0.0153$				ANOVA: microsite × date, $p = 0.0007$			
	0–15 cm	15–30 cm	30–50 cm	50–86 cm	June 1998	Sept 1998	April 1999	May 2000
LELA	18.3 (17.0–19.6)	15.8 (13.4–18.3)	4.4 (2.7–6.4)	0.4 (0.1–0.9)	5.5 (4.5–6.6)	9.0 (7.0–11.3)	6.9 (5.3–8.7)	9.0 (7.7–10.4)
ELEL	14.5 (13.6–15.4)	10.5 (8.7–12.6)	0.9 (0.5–1.4)	0.1 (0.1–0.2)	5.2 (4.2–6.2)	5.0 (4.6–5.5)	3.3 (2.5–4.2)	4.0 (3.1–4.9)

Abbreviations: LELA – *L. Latifolium*; ELEL – *E. elongata*. Primary data are means of replications by date, depth and microsite. Only statistically significant interactions including microsite are presented for which confidence intervals (95%) are displayed in parentheses.

Table 5. Correlation matrixes for *L. latifolium* (top) and *E. elongata* (bottom). Data are pooled over sampling date and soil depth

	% OC	% N	C/N ratio	Urease	Glutaminase	Asparaginase	Amidase
% OC	1						
% N	0.94***	1					
C/N ratio	−0.08	−0.34*	1				
Urease	0.84***	0.75***	0.16	1			
Glutaminase	0.91***	0.86***	0.03	0.89***	1		
Asparaginase	O.89***	0.84***	−0.03	0.70***	O.82***	1	
Amidase	0.94***	0.87***	0.01	0.90***	0.95***	0.84***	1
% OC	1						
% N	0.90***	1					
C/N ratio	0.44**	0.11	1				
Urease	0.76***	0.73***	0.35*	1			
Glutaminase	0.69***	0.48**	0.47	0.36*	1		
Asparaginase	0.83***	0.81***	0.25	0.59***	0.60***	1	
Amidase	0.93***	0.87***	0.38	0.82***	0.54***	0.85***	1

* Denotes $p \leq 0.05$, $p \geq 0.01$; ** Denotes $p < 0.01$, *** Denotes $p < 0.001$.

and available N for *L. latifolium* broke down when enzyme activities were correlated with net N mineralization potential (Figure 2). Indeed, all four enzymes were negatively correlated with net N mineralization in the 0–15 cm depth increment and overall had much lower R^2 values. In this case, enzyme activity relationships with net N mineralization were much stronger for *E. elongata*.

Table 6. C/N ratios, by soil depth, for sites occupied by *L. latifolium* and *E. elongata*

Soil depth (cm)	*L. latifolium*	*E. elongata*
0–15	11.8 (3.7)	12.8 (3.0)
15–30	12.8 (3.0)	11.7 (2.9)
30–50	11.1 (3.3)	10.6 (3.8)
50–86	10.9 (3.4)	9.2 (4.2)

Standard deviations shown in parentheses.

Discussion

The data support the working hypothesis; *L. latifolium* modifies the soil to favor its own growth and survival. Plants exert considerable control on many facets of soil development including nutrient cycling, organic matter quantity and quality, and mineral weathering (Kelly et al., 1998; Miles, 1985; Ulery et al., 1995). Plants can be considered 'ecosystem engineers' in the sense that they modify the physical and chemical state of the soil and thereby engender qualities favorable or unfavorable to other species and/or themselves (Jones et al., 1994; Van Breemen and Finzi, 1998). *L. latifolium* increases soil pools of available N and net N mineralization potentials relative to *E. elongata* plant communities it is replacing. It does so even though C:N ratios are statistically similar between the two plant microsites. Moreover, the available water holding capacity of soils occupied by the two species are statistically similar (*L. latifolium* = 181 g kg^{-1} sd. 6.2; *E. elongata* = 173 g kg^{-1} sd. 5.8). Specific plant species and communities can differentially affect the soil N cycle (Bolton et al., 1990; Chen and Stark, 2000). Why would increasing availability of N favor *L. latifolium* invasion? Of all factors which explain ecosystem invasibility, the seasonal timing and magnitude of available soil N is robust (Padgett and Allen, 1999; Tilman, 1990; Vitousek, 1990). In the environments *L. latifolium* is invading, water is generally not limiting; N is the keystone nutrient which enables rapid growth. Another facet in the competitive strategy of *L. latifolium* is its ability to explore deeper N sources than vegetation it is competing with as evidenced by elevated available N in the 50–86 cm depth increment. Exploration of deeper nutrient supplies is a competitive advantage to some invasive weeds (Shelley and Larson, 1995).

Strong positive correlations between soil amidohydrolase activities and available soil N suggest that

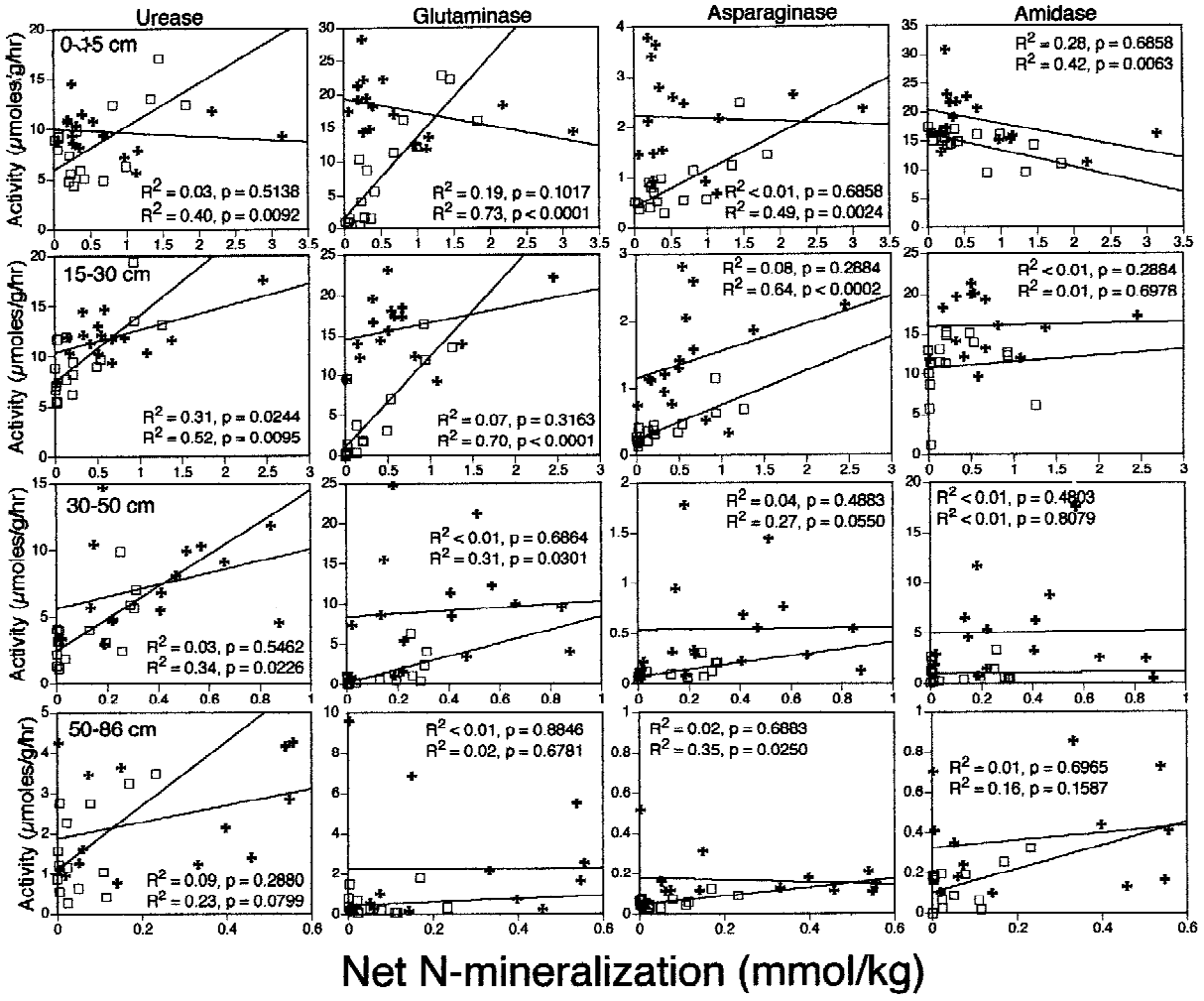

Figure 1. Relationships of enzyme activities of urease, glutaminase, asparaginase, and amidase to KCl-extractable (available) N. Data are pooled over sampling date and separated by soil depth. Symbols are + = *L. latifolium*, □ = *E. elongata*. For each panel, R^2 values refer to *L. latifolium* and *E. elongata*, respectively.

L. latifolium somehow facilitates greater quantities of these enzymes, relative to species being replaced. Plant communities can influence soil enzyme activities (Pancholy and Rice, 1973) and enzyme activity can proxy for N mineralization potential (Killham and Rashid, 1980). How does *L. latifolium* increase amidohydrolase activity? Mechanistically this may occur by root exudation and turnover and/or fostering a greater abundance of bacterial species which manufacture amidohydrolases (Skujins, 1967). Initial research in my lab suggests roots of *L. latifolium*, on a per weight basis, have similar urease and amidase activity and much less asparaginase and glutaminase activity than surface soil values beneath *L. latifolium*. This finding suggests *L. latifolium* must foster microbial organisms to produce elevated asparaginase and glutaminase activities. However, there must be linkages and feedback mechanisms for all enzyme sources to explain the strong correlation among the activities of urease, asparaginase, glutaminase, and amidase.

If amidohydrolases were the sole rate controlling step in N-mineralization; then one should obtain strong positive correlation between enzyme activities and net N mineralization (Abdel Magid and Tabatabai, 1991). The general lack of correlation suggests another enzyme(s), not measured in this study, is/are the rate controlling step for N-mineralization in *L. latifolium* occupied systems. In future work, a potential rate controlling enzyme arylamidase will be evaluated (Acosta-Martinez and Tabatabai, 2000).

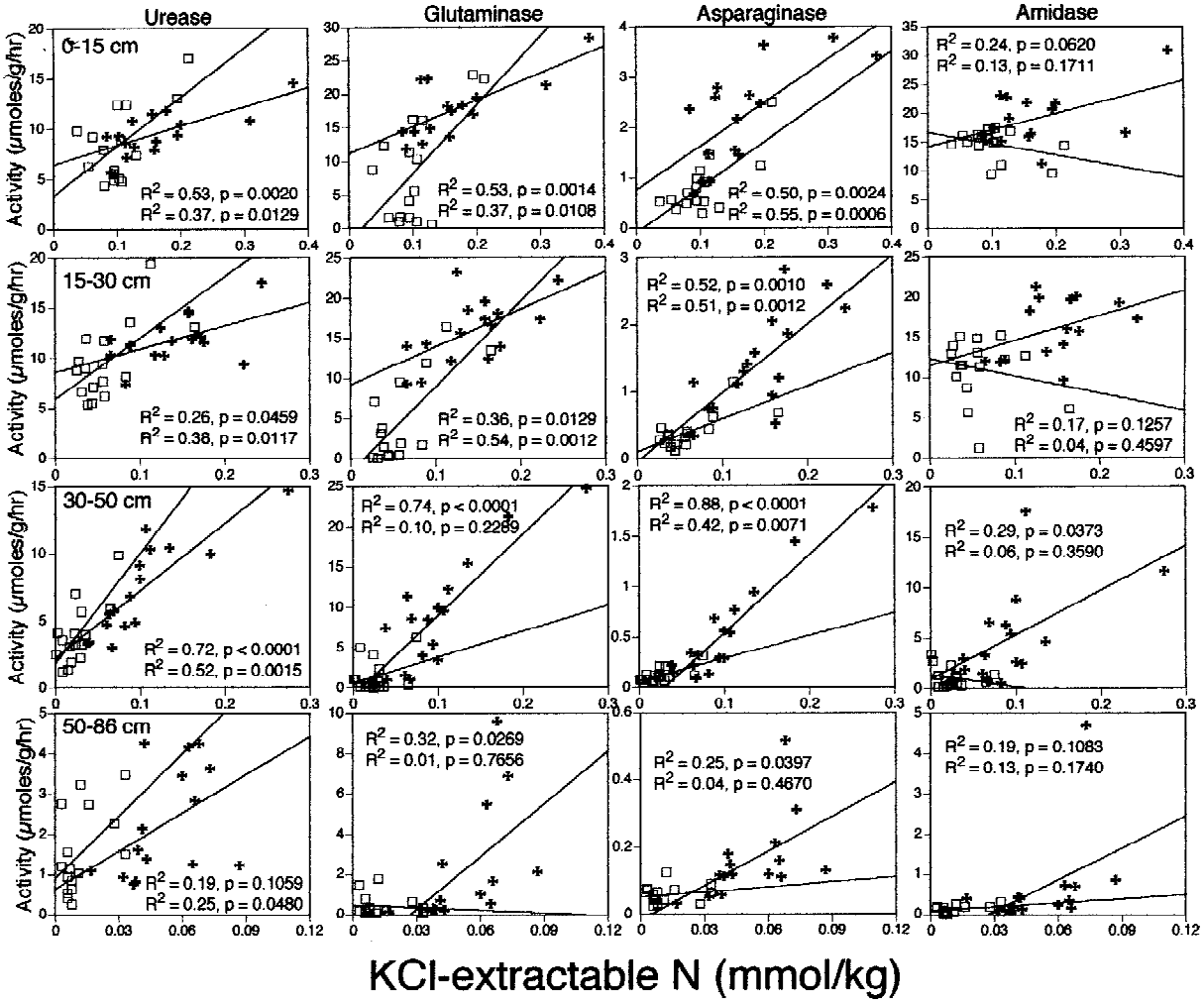

Figure 2. Relationships of enzyme activities of urease, glutaminase, asparaginase, and amidase to net 30 day aerobic mineralization potentials. Data are pooled over sampling date and separated by soil depth. Symbols are + = *L. latifolium*, □ *E. elongata*. For each panel, R^2 values refer to *L. latifolium* and *E. elongata*, respectively.

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